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Body Size and Differential Mating Success between Males of Two Populations of the Mediterranean Fruit Fly[1]

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ABSTRACT: Mate preference experiments were conducted between males from two populations of the Mediterranean fruit fly, *Ceratitis capitata*, to investigate the effect of body size on mating success. The results of the experiment indicate that increased body size of males cannot be equated with mating success. In the lek behavior phase, physical encounters between males for possession of a preferred territory seem to favor a male with a larger body size. However, males from one of the populations were twice as successful in mating with females of either population than males from the other population despite their significantly smaller body size. Thus, it appears that while size may possibly be correlated with intrasexual selection and the establishment of a dominance hierarchy within the lek, courtship performance is st'll the most important criterion for mating success in the medfly.

MATING, AS AN ESSENTIAL ACT in sexually reproducing species, can be divided into two basic processes. The first process functions to bring the two sexes into close proximity, and the second process, courtship, leads to copulation. For most animals that form only temporary associations during mating and make little or no investment beyond that of providing gametes, both processes are essential components of the mating system.

The lek system is one such mating system in which both processes are essential components. A *lek* is defined as an aggregation of territories used by males for the sole purpose of mating (Wilson 1975). A *territory* is a position within a lek defended by a male for courtship and mating. The lek therefore provides a localized assembly of males to which females in search of a mate are attracted, and functions as a means of bringing the two sexes into close proximity. Furthermore, the males that participate in lek formation are in competition with one another (as indicated by male–male interactions) in securing a "preferred" territory to which receptive females are attracted. Though the attraction of females to the lek is a concerted effort of all males within the lek, not all of the males are successful in mating (Arita and Kaneshiro 1985).

In the lek system, a male not only has to compete against other males to become part of the lek population, but in addition, he must be able to occupy a preferred territory in order to increase courtship opportunities. Once a female arrives in his territory, the male's courtship ability determines his mating success. Thus, reproductively successful males are males that not only are able to defend a preferred territory, but also are able to lower the receptivity threshold of the female through performance of an adequate courtship pattern.

Recent outbreaks of the Mediterranean fruit fly, or medfly, *Ceratitis capitata* (Wiedemann), have led to a resurgence of research on the basic biology of this insect to obtain important information for the development of effective control programs. In earlier reports on the mating behavior of the medfly, detailed descriptions of the various behavioral components involved in mating were presented, but most failed to recognize the lek system

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(Back and Pemberton 1918, Feron 1962, Martelli 1910). The first reference to the existence of lek behavior in this species was provided by Prokopy and Hendrichs (1979) with their studies of medflies released on a field-caged coffee tree. Arita and Kaneshiro (1983, 1985) provided further descriptions of the lek system and separated the mating behavior of the medfly into two phases: (1) lek behavior and (2) courtship.

Research on other lek species has indicated that body size may be correlated with a male's ability to acquire and defend a territory (Borgia 1980, Davies and Halliday 1978, Ryan 1980). Body size also has been implicated in mating success among lekking males (Bradbury and Gibson 1983), and, in fact, Burk and Webb (1983) indicate that increased body size in a related species of tephritid is a contributing factor in mating success. However, some recent evidence indicates that body size may not necessarily be correlated with mating success (Cohet and David 1980, Knapton 1985).

On the island of Hawaii, a population of *Ceratitis capitata* was found to be significantly larger in body size than a geographically separate population of *C. capitata*. Mate preference experiments were conducted between the males from these two populations to determine the possible effects of body size on mating success in this species.

MATERIALS AND METHODS

Flies used in this study were reared from substrates collected from two sites on the island of Hawaii. One population was reared from Jerusalem cherry, *Solanum pseudocapsicum* L., collected in Kipuka Ki, Volcanoes National Park, and the other population was reared from Arabian coffee, *Coffea arabica* L., collected on the Kona coast just above Kealakekua Bay.

The fruits from these areas were collected, brought into the laboratory, and set into rearing containers. After 10 days at a constant temperature of 24°C, pupae were collected from the rearing containers and placed into holding cages until adult emergence. Within 24 hr of emergence, the flies were sexed and placed into cages that were provided with adult media (a honey and protein hydrolysate mixture) and water. All adults were aged for at least 7 days prior to experimental use to ensure sexual maturation (Arita 1982). Males were color coded for identification purposes prior to experimental use by chilling them at 0°C for a few minutes and then applying a small spot of Testor's enamel to the mesonotum.

Two males (one from each population) were placed into a 23 × 23 × 23-cm glass cage supplied with adult media, water, and a potted *Syngonium* plant. The two males were given a 24-hr period to acclimate to the cage conditions, during which time all male–male encounters on each leaf of the plant were recorded. Following the acclimation period, a virgin female from one of the populations was placed into the cage with the two males, and her choice of mate was recorded. Forty-four females from the Volcano population and 39 females from the Kona population were tested for mate preference in cages with Kona and Volcano males.

Once the female mated, the trio (successful male, unsuccessful male, and female) was removed from the cage, and the thoracic lengths of all three individuals were measured. The length of the thorax was measured along the median plane of the notum. The thorax was chosen for measurement and size comparison because there is less variability in this body region as opposed to total body weight or other parts of the body that may be influenced by nutrition after emergence. Data on body

TABLE 1

NUMBER OF MATINGS BETWEEN TWO POPULATIONS OF *Ceratitis capitata* IN MATE PREFERENCE EXPERIMENTS (TWO MALES AND ONE FEMALE)

ORIGIN OF FEMALE	n	KONA MALE	VOLCANO MALE	C*
Kona	39	26 (0.67)	13 (0.33)	2.12
Volcano	44	30 (0.68)	14 (0.32)	−2.39
Totals	83	56	27	

* At the 5% confidence interval, the null hypothesis that mating is random is accepted if $-1.96 < C < +1.96$.

size relative to mating success were compared by Mann–Whitney test (Sokal and Rohlf 1969).

A statistical test of significance was calculated for each reciprocal combination (Table 1) by applying the female for the test of proportions, $C = 2n(\hat{p} - 0.5)$, where $\hat{p}$ is the mean of the sampling distribution. At the 5% confidence interval, the null hypothesis that mating is random is accepted if $-1.96 < C < +1.96$.

RESULTS

The results of the mate preference tests are presented in Table 1. The data indicate that Kona females chose males from their own population twice as often as males from the Volcano population. Similarly, Volcano females chose Kona males twice as often as males from their own population. These results suggest that the Kona males performed some aspect of the overall mating process in a way that females from both populations preferred (as compared to the Volcano males), regardless of the size of the female.

The thoracic lengths are presented in Tables 2 and 3. Not only was there a significant size difference between the males of the two populations, but when comparing body size and mating success, the successful Kona males were significantly smaller than the unsuccessful Volcano males in competition for Kona females ($U = 4.524$; $p < 0.05$; 26, 26). Also, the successful Volcano males were significantly larger than the unsuccessful Kona males in competition for Kona females ($U = 4.433$; $p < 0.05$; 13, 13). Thus, Kona males were selected as mates twice as often by Kona females even though they were an average of 9.3% smaller in body size than Volcano males. Volcano males chosen by Kona females as mates were an average 19.3% larger than the Kona males.

Similar percentages were obtained for Kona males ($U = 5.655$; $p < 0.05$; 30, 30) and Volcano males ($U = 4.179$; $p < 0.05$; 14, 14) chosen as mates by Volcano females. Kona males were chosen twice as often by Volcano

TABLE 2

AVERAGE THORACIC LENGTHS (mm) OF MALES SUCCESSFUL AND UNSUCCESSFUL IN MATING WITH KONA FEMALES

ORIGIN OF MALE	UNSUCCESSFUL MALES	SUCCESSFUL MALES	FEMALES
Kona	1.99 ± 0.03 SD	2.08 ± 0.03 SD	1.99 ± 0.04 SD
Volcano	2.43 ± 0.01 SD	2.40 ± 0.02 SD	2.03 ± 0.07 SD

U (successful Kona males and unsuccessful Volcano males) = 4.524*
U (successful Volcano males and unsuccessful Kona males) = 4.433*

* Mann–Whitney test, significant at the 0.05 level.

TABLE 3

AVERAGE THORACIC LENGTHS (mm) OF MALES SUCCESSFUL AND UNSUCCESSFUL IN MATING WITH VOLCANO FEMALES

ORIGIN OF MALE	UNSUCCESSFUL MALES	SUCCESSFUL MALES	FEMALES
Kona	2.00 ± 0.04 SD	2.02 ± 0.04 SD	2.31 ± 0.02 SD
Volcano	2.40 ± 0.02 SD	2.48 ± 0.01 SD	2.37 ± 0.03 SD

U (successful Kona males and unsuccessful Volcano males) = 5.655*
U (successful Volcano males and unsuccessful Kona males) = 4.179*

* Mann–Whitney test, significant at the 0.05 level.

females even though they were an average of 14.4% smaller than Volcano males. Volcano males chosen as mates by Volcano females were an average of 17.6% larger than the Kona males.

DISCUSSION

Arita and Kaneshiro (1985) observed that certain territories within the lek of *Ceratitis capitata* are highly prized as courtship sites, and males that can successfully defend these preferred territories will have more opportunities to court females. However, in some instances, we observed that though a male may be occupying a preferred territory (as determined by the number of male–male encounters on each plant leaf), he is not necessarily more successful in mating. Thus, it appears that while a male's ability to occupy and defend a preferred territory may provide him more opportunities to encounter females, the final criterion for mating success is still dependent on his courtship abilities. The lek system in the medfly is therefore dependent first on acquiring a territory within the lek, and second on performing a courtship sequence satisfactory to the female. Based on the results of this experiment, it appears that Kona males must have (1) the ability to acquire a territory against larger Volcano males and/or (2) superior courtship abilities such that females do not seek out any other males once landing on a territory of a Kona male.

There are at least two possible explanations for the superior mating ability of the Kona males: (1) The two populations are geographically isolated, and thus inherent genetic differences may exist that are reflected in the quality of the Kona males' mating behavior. Such one-sided mate preference by females of two populations for the males of one population has already been demonstrated in other animals (Giddings and Templeton 1983, Kaneshiro 1983). (2) Chemical stimuli have already been implicated in both the lek phase (pheromone calling) and the courtship phase of the mating behavior (Arita and Kaneshiro 1985). Since one population was reared on coffee and the other population on Jerusalem cherry, differences in the larval medium may have affected the quality of the chemical stimuli, biasing the mate choice toward the Kona males reared out of coffee. Further experimentation with larval media may provide new insight into the role of environmental factors on mating success.

Clearly, an understanding of the complex mating system of natural populations of the medfly will greatly enhance our ability to develop a more effective control program. Whether the Sterile Insect Release Method or any other control method involving the use of laboratory-reared strains is utilized, it is essential that such strains be able to penetrate the natural lek system of this species. Questions still remain, however, about the sexual fitness of body size and whether females rely on other features of the complex mating pattern (i.e., courtship) to select the "best" male. Resource limitations during the larval stages greatly influence the body size of the adult stage in holometabolous insects, and thus genetic components of size and other fitness components in these organisms may have been masked. Thus, females that may encounter larger males more often than smaller males because of position in the dominance hierarchy still require the males to perform complex courtship displays. The results of this study indicate that characters other than body size are essential determinants of mating success of the males and that any attempts to improve the behavioral quality of laboratory-reared strains must include an assessment of the courtship abilities of the males.

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